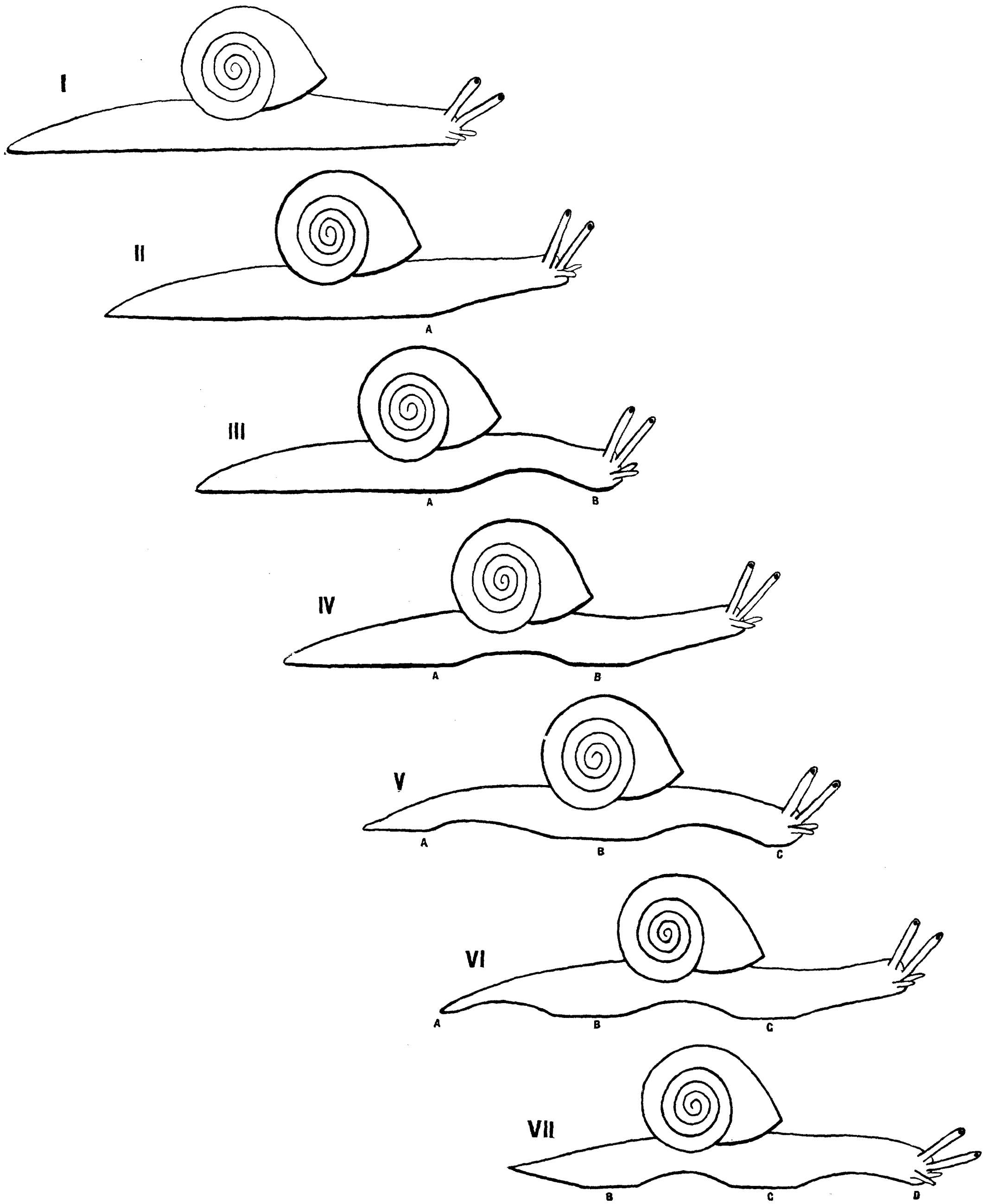
THE PHYSIOLOGY OF LOCOMOTION IN GASTEROPODS.

A. J. CARLSON.

While studying the physiology of the molluscan heart I incidentally observed in the snail a mode of locomotion which would seem to explain the mechanism by which the series of waves of contraction and relaxation of the sole of the gasteropod foot in locomotion are produced. The musculature of the foot and the ordinary movements of locomotion of land gasteropods by a series of alternating contractions and expansions, passing as waves over the sole of the foot in the postero-anterior direction, has been described by Simroth (1878, 1879).[1] Simroth's observations were made principally on *Helix* and *Limax*. In attempting to correlate the form and sequence of these waves of locomotion with the structure of the musculature of the foot Simroth concludes that they cannot be produced by the separate or combined contractions of the oblique and the transverse muscular strands. The cause of the extension of the foot is to be sought in the active extension of the longitudinal musculature; that is, when the muscle-cells making up these strands contract they elongate and decrease in thickness. These he therefore calls "extensile muskulatur" in contradistinction from the oblique and the transverse muscle, which is of the ordinary contractile type.

This theory of "extensile muskulatur" may explain the series of elongations of the foot in locomotion, but the question is, Is it true? The theory may without much difficulty be put to the experimental test by any one interested. Simroth does not show that the muscle-cells making up the longitudinal musculature of the foot increase in length and decrease in diameter on direct stimulation or on stimulation of the pedal nerves. A few ex-

[1] Simroth, H., "Die Thätigkeit der willkürlichen Muskulatur unserer Landsnecken," *Zeitschr. f. wiss. Zoöl.*, XXX., p. 166; "Die Bewegung unserer Landsnecken, hauptsächlich erörtert an der Sohle des Limax," *Zeitschr. f. wiss. Zoöl.*, XXXII., p. 284.



Locomotion of the snail. For description see text.

periments in that line would have convinced him of the fallacy of his theory. I have tested the longitudinal muscle of the foot in several gasteropods and my results go to show that there is no difference between the physiology of this muscle and that of any other muscle. On stimulation, either directly or through the motor nerves, the muscle-cells or strands of muscle-cells shorten and thicken in the usual way. These experiments may be performed with the greatest ease on the foot of *Pleurobranchæa*, as the foot musculature of this gasteropod is composed of a very loose meshwork of septa that may be separated the one from the other without sufficient injury to produce extreme contraction. In gasteropods with very compact foot this cannot be done, as the injury of dissection produces extreme contraction. But even when the foot musculature is greatly contracted direct stimulation

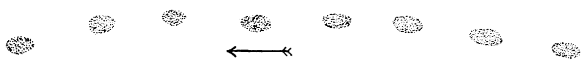


FIG. 1. Tracings, ½ natural size, of the tracks of a snail moving in the manner illustrated on previous page. The dotted areas are the areas covered by the mucus film. The arrow indicates direction of the motion. Medium-sized animal, moving rapidly.

with the induced electrical current produces, not an elongation, but a further shortening and thickening of the muscle. In no case does the stimulation produce elongation of the longitudinal muscle strands.

Jordan (1901)[1] rejects the theory of "extensile muskulatur" in accounting for the locomotion in the marine gasteropod *Aplysia*, and ascribes the relaxation or extension of the longitudinal muscle of the foot to the pressure of isolated bodies of the visceral fluid or blood. As evidence Jordan points to small reservoirs or lakelets of plasma in the strongly contracted foot. These lakelets are constricted off from the visceral cavity by the contraction of the muscular septa. A body of liquid thus cut off from the visceral cavity may serve to produce extension of the longitudinal muscle at its anterior border by the force of contraction of the oblique and transverse muscles at its posterior end. In this way we would have as many isolated bodies of

[1] Jordan, H., "Die Physiologie der Locomotion bei Aplysia limacina," *Zeitschr. f. Biologie*, XLI., p. 196.

blood being gradually pushed from behind forwards in the foot as there are areas of relaxation on the sole of the foot. The presence of isolated bodies of liquid in the strongly contracted foot is not a sufficient evidence that they are the factors in producing the waves of locomotion, as similar isolated bodies of liquid are also found in the musculature of the contracted mantle (*Aplysia*, *Pleurobranchæa*).

The arrangement of the muscle in the foot and the appearance of the sole of the foot in locomotion are so similar in all gasteropods that the mechanism by which locomotion is effected is in all probability the same in all. Simroth and Jordan missed the true explanation by not taking into account the part played by the musculature of the dorsal and lateral walls of the body cavity.

The mode of progression of the snail which furnishes the key to the solution is represented in the series of diagrams on page 2. Diagram I. represents the side view of the snail during ordinary locomotion. The edges of the foot touches the ground throughout the whole length of the animal, and a continuous trail of mucus marks the path of progression. When the animal changes this gait to that illustrated in diagrams II. to VII. the head is lifted from the ground and while pushed forward by the progression of the rest of the body the neck or successive portions of the anterior end is elongated and the diameter diminished as it leaves the contact with the ground. In a few seconds the anterior third of the animal comes to assume the position shown in diagram II. This elongated head end is being held clear of the ground at an angle of 20 to 30 degrees. All this while the animal progresses by means of the part of the foot still in contact with the ground. When the anterior one fourth or one third of the body has attained position II., the head bends down so that the very anterior end of the foot again comes in contact with the ground. The neck and anterior part of the body are bent to form an arch in the manner shown in diagram III. The distance from the ground to the highest point of the curve is from 2–4 mm. The posterior end of the body now appears literally to flow through this arch to the new point of contact (*b*), that is, as the posterior part of the body moves forward

the successive portions form their respective parts of the curve. The space of ground between *a* and *b* is not touched by the foot in any region of the body. While the middle third of the body is thus pushed and pulled forward, elongating, diminishing in diameter and bending away from the ground to form the arch *a–b* (diagram IV.), the head end repeats the performance of diagram II. The foot at the head end continues in contact with the ground only for a distance of one to one and a half centimeter. When the head and neck bend away from the ground, the neck elongates as before, and we have the anterior third of the body in diagram IV. in a position similar to that in diagram II., the head ready to bend down to make a new contact (*c*). The next stage is shown in diagram V. The middle third of the body has advanced to the second point of contact (*b*) and the arch stage or state of elongation and decrease in diameter is being assumed by the last third. The head end repeats the performance of dia-

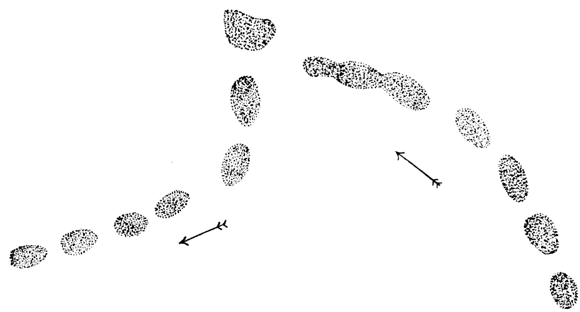


FIG. 2. Same as Fig. 1. Portions of the track of a large specimen moving slowly. ½ natural size.

gram II. and IV., till in VI. it is again elongated and raised from the ground. The snail has now traversed a distance equal to the length of its own body, so that only the extreme tail end of the foot touches the original contact (*a*). The tail end is very much reduced in diameter at this stage. As the head bends down to make the fourth contact (*d*) the tail end is being lifted high from the ground and pulled up to contact *b* in the manner shown in diagram VII. Further progression is simply a repetition of these phenomena. When the whole body has come into this mode of progression the foot is thus in contact with the ground

only at three points, the intervening parts being held in the position of arches clear of the ground. In some instances the foot may be in contact with the ground only at two places, as in diagram VI. the tail end may be lifted from the ground before the head bends down to make the next contact. At any one time there will thus be two regions of elongation and decrease in diameter of the body and three regions of shortening and thickening of the body and *vice versa*.

When moving in this manner the snail does not leave a continuous film of mucus along its path as in ordinary locomotion, but a trail like the ones represented in Figs. 1 and 2 on page 2. These figures are traced from the tracks made by the snails across the table, the surface of which was covered with a thin layer of dust. The arrows indicate the direction of the motion, the dotted areas are the places touched by the foot and hence covered with a film of mucus. Fig. 1 is a portion of the track of a snail of medium size moving straight ahead at a rapid rate. The areas of contact of the foot with the surface are smaller and the further apart the quicker the progression. Fig. 2 is taken from the trail of a larger snail moving slowly and not in a straight line. The areas of contact are larger and closer together, and may even fuse.

This mode of locomotion enables the animal to cover the ground much quicker than in the ordinary way, and it was always resorted to by the snail studied (*Helix dupetithouarsi*) when endeavoring to escape from an enemy. I observed it for the first time after having punctured the apex of the shell preparatory to injection of alkaloids into the animal. When replaced on the table the snail quickly emerged from the shell and started this gallop across the table. But the snail will make use of this mode of locomotion when not in the least injured. For some reason I never succeeded in making a specimen move in this manner across a surface covered with lampblack. If a smoked paper was placed in the path of a galloping snail the animal resorted to the ordinary locomotion on touching it. I have not observed this mode of locomotion in the slugs (*Limax*, *Ariolimax*) or in any of the marine gasteropods.

What is the mechanism of this mode of progression and in

what way does it differ from the ordinary locomotion ? Referring again to the diagrams on page 2 it is obvious that the series of changes of form and position of the anterior third of the body resulting in the position shown in diagram II. cannot be brought about by the musculature of the foot alone, even if aided by isolated bodies of liquid. The entire musculature of this end of the body must be brought into play. If the transverse and the oblique muscular strands contract gradually at successive levels from behind forwards simultaneous with the relaxation of the longitudinal muscle, this part of body would elongate and decrease in diameter just as actually occurs. The elevated position of the elongated head end is simply due to the greater relaxation of the longitudinal muscle in the foot than in the dorsum. The pushing forward of the head end is probably aided by the pressure of the viscera.

The bending down (or in any direction) of the head end is obviously a result of the contraction of the longitudinal muscle in the foot simutaneous with the relaxation of that in the dorsum. If we assume that the posterior half of the elongated head end retains the original contraction of the several muscle systems and that in the anterior half the foot contracts and the dorsum relaxes, we have the downward movement of the head and the formation of the arch. The passage of the middle third of the body through the ascending limb of the arch is simply the continuation of the processes of contraction of the transverse and oblique muscle and relaxation of the longitudinal muscle which brought about the elongation and elevation of the head end. The same muscular mechanisms which must act in the latter case suffice to account for the former. In the descending limb of the arch the relation of contraction and relaxation of the systems of muscles is reversed. The transverse and the oblique muscles relax and the longitudinal muscles contract, pulling that part of the body forward and down to point *b* (diagram II.). Friction is probably sufficient to prevent the head end being pulled backward instead of the body forward by this contraction. The lifting up and subsequent shortening and thickening of the tail end in diagrams VI. and VII. is simply a relatively sudden contraction of the dorsum of this part and subsequent contraction of all the

longitudinal muscle strands. By thus taking into account the entire body musculature, their coördinate contraction and relaxation suffice to account for these changes in form and position without having recourse to any "extensile muskulatur" or series of isolated bodies of liquid in the foot.

What has this mode of progression in common with the ordinary locomotion? In the chitons the dorsal shells prevent any considerable contraction and elongation of the dorsum. And even in ordinary locomotion of other marine gasteropods as well as of the pulmonates there is no appreciable elongation and shortening of the dorsum corresponding to the waves of locomotion on the sole of the foot. Nevertheless the peculiar mode of progression in the snail just described is probably only an exaggerated form of the ordinary locomotion. During ordinary progression the animal assumes its greatest length and smallest diameter; to account for this we need nothing further than the contraction of the transverse and the oblique muscles of the dorsal and lateral sides of the body. The waves of locomotion in the foot are diminutive representatives of the waves of relaxation and contraction illustrated in the diagrams on page 2. At the areas of relaxation the sole of the foot adheres closely to the ground, and between these points the sole is slightly elevated. Nevertheless a continuous layer of mucus covers the path of progress, as the areas of contact are close together and subsequent portions of the foot occupying the same area is pulled forwards a little so as to finally touch the preceding area of contact. There can be little doubt that the area of contact of the foot with the ground in any region serves as a fixed point through friction and acting on this the contraction of the longitudinal muscles of the foot pulls the neighboring portion of the body forwards.

Physiological Laboratory,
University of Chicago.